



# Biogeography and macroecology of phorid flies that attack fire ants in south-eastern Brazil and Argentina

P. J. Folgarait<sup>1\*</sup>, O. Bruzzone<sup>1</sup>, S. D. Porter<sup>2</sup>, M. A. Pesquero<sup>3</sup> and L. E. Gilbert<sup>4</sup>

<sup>1</sup>Centro de Estudios e Investigaciones, Universidad Nacional de Quilmes, Buenos Aires, Argentina, <sup>2</sup>USDA-ARS, Center for Medical, Agricultural and Veterinary Entomology, Gainesville, FL, USA, <sup>3</sup>Departamento de Ecología e Biología Evolutiva, Universidade Federal de São Paulo, São Paulo, SP, Brazil and <sup>4</sup>Section of Integrative Biology and Brackenridge Field Laboratory, University of Texas, Austin, TX, USA

## ABSTRACT

**Aim** Saevisima group fire ants, *Solenopsis richteri* and *S. invicta*, have become serious pests when introduced from Argentina and Brazil to other continents. In South America, *Solenopsis* are distributed across a great variety of habitats and climates. In North America, *S. invicta*, introduced free of phorids, now ranges from coast to coast in the south. Success in introducing particular *Pseudacteon* as agents for the biological control of fire ants has varied across climatic zones. We aimed at assembling all the information about fire ant phorids from Argentina and Brazil, to estimate their richness and geographical ranges, to perform a climatic analysis for these distributions, to define groups and climate-based communities, and to test and elucidate Rapoport's biogeographical rule.

**Location** Argentina and Brazil (South America).

**Methods** From field and museum collections and historical records, we developed a database of fire ant-specific phorids throughout their known geographical range. A total of 123 sites with values for 15 climatic variables were mapped between 10° and 38° SL and between 35° and 65° C WL for the presence/absence of phorids. We calculated species richness across all sites combined, and for each phytogeographical region, using rarefaction curves, and ICE and Mmean estimators. We calculated mid-latitudinal points, geographical ranges and areas for each species. The correlation between mid-latitudinal point and ranges/areas was tested against a null model generated from the randomization of the raw distributional data. We used several types of multivariate analyses to distinguish groups of phorids by phytogeographical regions, hosts and climate, to find gradients of climate throughout the studied area, to define phorid communities in terms of their relationships with gradients of climate, and to test a mechanism for Rapoport's rule.

**Results** Richness estimations using ICE and Mmean estimators were similar or higher than the observed values depending on the phytogeographical region. Cluster multivariate analyses based on climatic, phytogeographic and host data revealed distinct groupings of *Pseudacteon*. The 'cerrado' group was confined to tropical savanna areas. A more 'widespread' group included 'Chaco' and 'Maritime' subgroups defined by their respective association with extreme temperatures or precipitation. Ordination multivariate analyses showed (1) two climatic gradients throughout the study area: one of temperature and the other of precipitation, and (2) that climatic variables significantly explained the observed assemblages of phorids. Positive and negative signs of the eigenvalues from the main axes of a canonical correspondence analysis allowed us to define eight communities whose geographical distribution resembled that of

\*Correspondence: P. J. Folgarait, Centro de Estudios e Investigaciones, Universidad Nacional de Quilmes, Roque Saenz, Peña 180, Bernal B1876BXD, Buenos Aires, Argentina. E-mail: pfolgarait@unq.edu.ar

phytogeographical regions. We found a significant and positive correlation between geographical areas and mid latitudinal points, and furthermore, the Mantel test based on climatic variables suggested a mechanism for Rapoport's rule applying in the case of *Pseudacteon*.

**Main conclusions** *Pseudacteon* species with greater mid-latitudinal points occupy broader geographical areas and confront more stressful environmental conditions. Because the composition of *Pseudacteon* communities is largely determined by climatic variables, the correspondence between climates at sites of origin vs. sites of release should be an important consideration in choosing specific phorids for biocontrol efforts.

### Keywords

Biological control, black fire ants, climate, geographical distribution, parasitoids, phytogeography, *Pseudacteon*, Rapoport's rule, red fire ants, species richness.

### RESUMEN

**Metas** *Solenopsis richteri* y *S. invicta*, dos miembros de las hormigas de fuego del grupo Saevisima, se han tornado serias plagas después de ser introducidas desde Argentina/Brasil a otros continentes. En Sud América, estas especies, así como otras *Solenopsis*, se encuentran distribuidas a lo largo de una gran variedad de habitats y zonas climáticas. En Norte América, *S. invicta*, que fue introducida sin su fauna parasitoide, ahora se distribuye de costa a costa en el Sur de ese país. El éxito de la introducción de los fóridos *Pseudacteon* como una estrategia de control biológico ha variado dependiendo de las zonas climáticas. Nuestro objetivo fue juntar toda la información sobre los fóridos parasitoides de las hormigas de fuego de Argentina y Brasil, para estimar su riqueza y rangos geográficos, para realizar análisis climáticos de sus distribuciones, para definir grupos y comunidades climáticas, y para poner a prueba la regla de Rapoport y un mecanismo que la explique.

**Ubicación** Argentina y Brasil (América del Sur).

**Métodos** Construimos una base de datos de los parasitoides específicos de las hormigas de fuego a lo largo del rango geográfico conocido, a partir de datos de colectas de campo, de colecciones de museos, y de registros históricos. Ubicamos en un mapa entre los 10° y 38° LS y entre los 35° y 65° LO, los 123 sitios donde se registraron los parasitoides; en ellos además asignamos los valores correspondientes de 15 variables ambientales. Calculamos la riqueza para toda la región así como para cada provincia fitogeográfica, usando curvas de rarefacción con los estimadores ICE y Mmean. Calculamos los puntos latitudinales medios, los rangos geográficos, y las áreas de cada especie. La correlación entre el punto latitudinal medio y los rangos/áreas fue puesta a prueba con la generación de un modelo nulo producto de la aleatorización de las especies. Usamos distintos tipos de análisis multivariados para distinguir grupos de fóridos por regiones fitogeográficas, huésped y clima, para encontrar gradientes de clima a lo largo del área estudiada, para definir comunidades de fóridos en relación al clima, y para poner a prueba un mecanismo para la regla de Rapoport.

**Resultados** Las estimaciones de riqueza, usando ambos estimadores, fue similar o más alta a la observada dependiendo de las provincias fitogeográficas. Los análisis de clasificación multivariados basados en provincias fitogeográficas,

huéspedes y clima, revelaron distintos agrupamientos de *Pseudacteon*. El grupo del 'Cerrado' estuvo confinado a ambientes de savanas. El grupo de 'Amplia Distribución' incluyó al sub-grupo del 'Chaco' y al 'Marítimo' debido a su respectiva asociación con la temperatura y precipitación. Los análisis multivariados de ordenamiento mostraron (1) dos gradientes climáticos en el área de estudio, uno de temperatura y otro de precipitación, (2) que las variables climáticas explicaron significativamente el ensamble de fóridos observado. Los signos, positivos y negativos, de los autovalores de los tres ejes principales del análisis de correspondencia canónica nos permitió definir ocho comunidades cuya distribución geográfica se parecía a la de las provincias fitogeográficas. Encontramos una correlación positiva y significativa entre las áreas geográficas y los puntos latitudinales medios, es más, el Test de Mantel basado en las variables climáticas permitió identificar un mecanismo para este ensamble de *Pseudacteon*.

**Conclusiones principales** Las especies de *Pseudacteon* con puntos latitudinales medios mayores ocupan áreas geográficas más grandes y confrontan condiciones de stress climático mayores. Dado que la composición de las comunidades de *Pseudacteon* está en su mayor parte determinada por variables climáticas, la correspondencia climática entre el sitio de origen y el sitio de liberación de los parasitoides debería ser una consideración importante para la selección de especies de fóridos para el control biológico.

#### Palabras claves

Clima control biológico, distribución geográfica, fitogeografía, hormigas de fuego negras, hormigas de fuego rojas, parastoides, *Pseudacteon*, regla de Rapoport, riqueza.

## INTRODUCTION

Macroecology is concerned with understanding species and communities at large spatial and temporal scales (Brown, 1995; Gaston *et al.*, 1998). The occurrence of a number of macroecological patterns has been documented, including regularities in frequency distributions, correlates of abundances, patterns of energy use, variation of geographical ranges, body sizes and species richness (Blackburn & Gaston, 2001). Most macroecological studies to date have been based on mammals and birds. Much less has been explored with parasitoids (Gauld, 1986; Quicke & Kruft, 1995), ants (Farji Brener & Ruggiero, 1994; Sanders, 2002) or host–parasitoid relationships (Hawkins, 1990; Sime & Brower, 1998; Stadler, 2002).

The analysis of the relationship between a host and a parasitoid can be explored from different perspectives and scales. When hosts are pests, the macroecological study of such relationships acquires a practical dimension: for example, knowing the geographical distribution of a natural enemy species can generate hypotheses about its physiological amplitude. Further, recognizing biotypes of natural enemy species adapted to particular environments can increase the probability of appropriately matching prospective biocontrol agents to exotic environments.

In this study we focus on patterns in the distribution of dipteran parasitoids (Phoridae: *Pseudacteon*) of fire ants (Porter & Pesquero, 2001; Brown *et al.*, 2003) from Argentina and Brazil. Many species of ants are attacked by host-specific phorids (Disney, 1994; Folgarait *et al.*, 2002). These parasitoids oviposit an egg into the body of the ant host. The victim is killed as the larvae develop (Porter, 1998). Two species of fire ants, *Solenopsis richteri* and *S. invicta*, native to Argentina, have become serious pests since being introduced into North America. In their native ranges, these ants are attacked by c. 20 species of flies in the genus *Pseudacteon*. These flies impact their host directly through mortality (Morrison *et al.*, 1997) or indirectly through reducing worker foraging rates by as much as 77% (Feener & Brown, 1992; Folgarait & Gilbert, 1999).

Knowledge about the richness of this group is recorded only at the local level and for few communities (Fowler *et al.*, 1995; Pesquero *et al.*, 1996; Orr *et al.*, 1997; Folgarait *et al.*, 2003). Although species richness is an obvious measure of diversity, it is elusive, as more species will be recorded as additional samples are taken, especially so for diverse taxa (May, 1988; Bunge & Fitzpatrick, 1993). The expectation in any biodiversity study is that at some point in a species accumulation curve a plateau or asymptote will be reached where no further taxa

are added despite increasing the sampling effort (Willott, 2001).

Study systems that need richness estimators are those that are far from reaching the asymptote (i.e. insects generally; Fisher, 1999). For such cases estimators provide, at best, lower bound estimates of species richness (Gotelli & Colwell, 2001). In such studies, standardization of sampling effort is accomplished by a curve-smoothing process based upon repeated rarefaction curves (Gotelli & Colwell, 2001). Rarefaction curves represent the means of repeated Monte Carlo re-sampling of all pooled samples randomly accumulated in many iterations. There are numerous estimators of the asymptote with nonparametric estimators typically considered more promising than parametric ones for using information on the distribution of rare species (Colwell & Coddington, 1994). Finally, estimation of the total number of species by extrapolation, in combination with rarefaction curves, provides the best strategy for comparing observed data on richness to expectation for the region (Gotelli & Colwell, 2001; Longino *et al.*, 2002).

The value of macroecological analysis is enhanced if underlying mechanisms of the patterns are understood. We noted from our preliminary data that *Pseudacteon* flies in South America seemed to fit the macroecological pattern known as Rapoport's rule (Stevens, 1989), which predicts an increase in the latitudinal distributional range of a species as a positive function of the mean latitude of its geographical distribution. There are many mechanisms proposed to account for this pattern (Brown, 1995). Among the most relevant to predicting establishment success of introduced exotic species or biotypes is that species existing at higher latitudes have adapted to harsher climatic conditions than those at lower latitudes. Simply stated, progressively greater seasonality endured by a species throughout the year will be similar to the conditions that the species may encounter throughout its latitudinal range. Thus, a temperate species could be able to live in a greater range of habitats than a related species living at tropical latitudes.

Evidence to support Rapoport's rule is controversial (Gaston *et al.*, 1998). Methodological problems could be responsible for some apparent departures from the assumed pattern (Gaston *et al.*, 1998; Rohde, 1999; Ruggiero, 1999; Ashton, 2001). In this work we tried to avoid some of these previously recognized problems. First, we employ a null model approach (Colwell & Hurtt, 1994; Gotelli & Colwell, 2001; Koleff & Gaston, 2001) to generate from the observed data a random distribution of species throughout the range. Secondly, we took steps to eliminate the effect of continental shape (Lyons & Willig, 1997). Thirdly, we avoided the autocorrelation of data by considering each species as an independent sampling point (Rohde *et al.*, 1993). Finally, we automatically reduced the phylogenetic effect by working with species of one genus, *Pseudacteon*, all of which share the same basic life history and host group.

With respect to the potential application of our data, we are interested in determining whether Rapoport's rule indeed

holds true for the *Pseudacteon* parasitoid system, and if so, to discover underlying mechanisms for the pattern, particularly those related to climate. However, because univariate analyses between climate and distribution of each natural enemy species would have little efficiency for describing patterns of multiple species and climatic variables (Legendre & Legendre, 1998), we analysed simultaneously the geographical distribution of ant-attacking phorids in concert with climate, habitat (phytogeographical regions) and availability of potential hosts. Because all variables of interest interact, a multivariate approach is fundamental to understand the response of a group of similar parasitoid species to climatic gradients. A local scale *Pseudacteon* community analysis (Folgarait *et al.*, 2003) allowed us to predict that there would be a correspondence between climate and phorid communities.

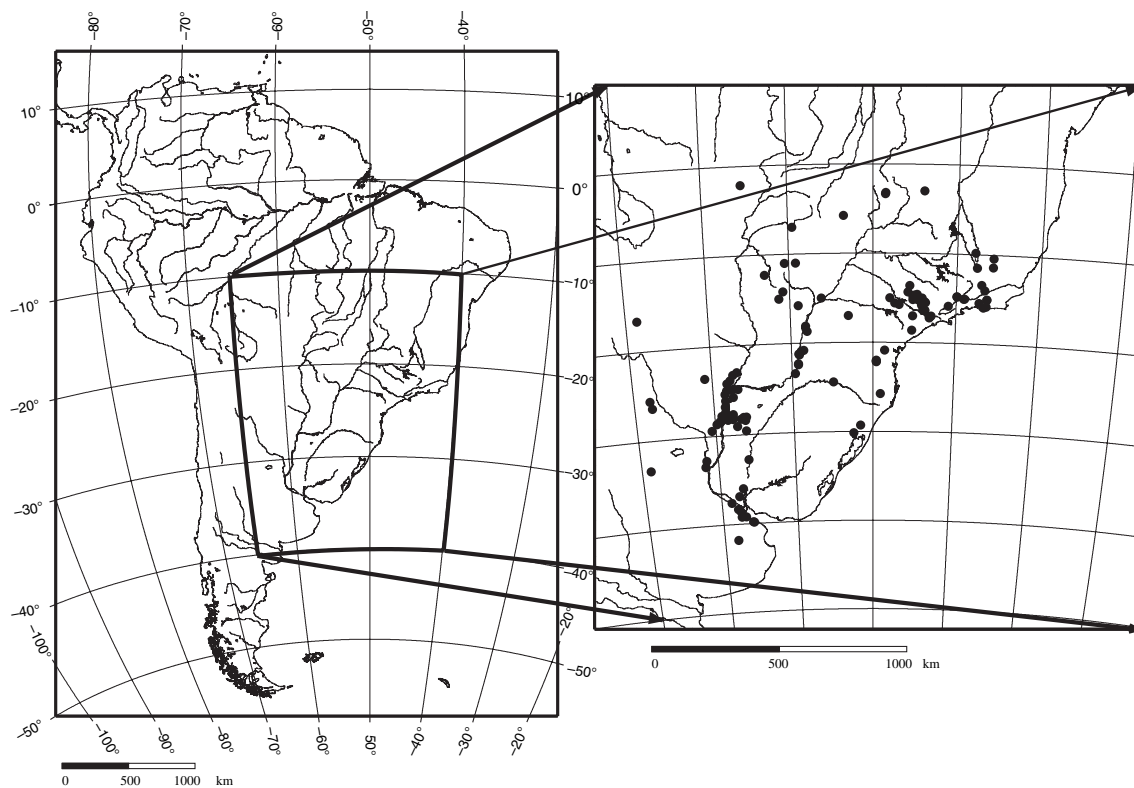
Despite the great interest that *Pseudacteon* phorids have generated with respect to their potential in biological control of exotic fire ants (Porter, 2000; Gilbert & Patrock, 2002), there is no compilation of the geographical distribution of the species that has been collected, nor of the climatic correlates that could explain such distributions (for a local community study see Folgarait *et al.*, 2003). Thus we were motivated to organize all the known, but scattered information on phorid parasitoids specific of *Solenopsis* from Brazil and Argentina with the goals of (1) estimating the species richness of these parasitoids within their known area of distribution and by phytogeographical regions, (2) delineating the ranges of geographical distribution of these parasitoids, and (3) analysing possible mechanisms that can account for the geographical distributions. To accomplish these goals we use three approaches: a biodiversity analysis to obtain richness information, a climatological analysis to obtain the climatic variables associated with the distributional ranges, and a macroecological analysis to test for Rapoport's rule and to identify possible mechanisms that can account for it.

## MATERIALS AND METHODS

### Data collection and management

The data for our analysis of phorid distributions consists of (1) our field samples of *Pseudacteon* taken as they attack *Solenopsis* ants at disturbed mounds and/or baits and (2) from historical records in the literature (Borgmeier, 1968; Orr *et al.*, 1995; Gilbert & Morrison, 1997) and (3) from museum collections. These records were at specific mapped locations between 10° and 38° S latitude and between 35° and 65° W longitude (Fig. 1), which correspond to the total latitudinal and longitudinal extent known for each of the 20 *Pseudacteon* species recorded. Because sampling efforts varied widely among the 123 sites, data for each *Pseudacteon* species were reduced to presence vs. absence at each location. Thus we use the term species richness rather than diversity in referring to the biogeographical patterns observed.

In addition to our map of *Pseudacteon* phorid occurrence, we also recorded the occurrences of all potential host species



**Figure 1** Map of South America. Collecting sites are enclosed within the square encompassing 10° and 38° S latitude and 35° to 65° W longitude. Each of the 123 *Pseudacteon* collecting sites are denoted by a black circle within the blow up of the region.

within the Saeviissima group, genus *Solenopsis* (Trager, 1991). The study region included 12 such species of *Solenopsis*, at least seven of which are known hosts of those *Pseudacteon* phorids included in this analysis.

Climatic data were obtained from Rudloff (1981), NOAA (1991) and Servicio Meteorológico Nacional (1992). Precise geographical information on each meteorological station was recorded and entered into the climatic data matrix. Data recorded from these stations included 15 variables: (1) thermal amplitude, (2) vapour pressure deficit (VPD) of the driest month, (3) mean annual VPD, (4) mean annual relative humidity (RH), (5) RH of the driest month, (6) number of months with precipitation < 10 mm, (7) number of months with precipitation < 30 mm, (8) mean annual precipitation, (9) absolute maximum temperature, (10) mean maximum temperature of hottest month, (11) mean temperature of the hottest month, (12) mean temperature of the coolest month, (13) mean minimum temperature of the coolest month, (14) absolute minimum temperature, (15) mean annual temperature.

These climatic data were entered into a site-by-climatic variable matrix encompassing the 123 sites and 15 variables. As climate data were not available for each sample locality, we used data from the closest available monitoring station in a similar ecological setting. Because we lacked uniformly dispersed spatial data, we were not able to use Kriging to create interpolated maps of climatic data (Isaaks & Shrivastava,

1989). Thus, for each of the 15 climatic variables we created interpolated contour maps using the inverse distance squared method incorporated in Surfer 8.0 software (Golden Software, 2001). These maps were then overlaid with maps of phorid distribution and integrated using mapping tools (GMT) (Wessel & Smith, 1995) in order to visualize patterns and develop hypotheses which were addressed later by formal multivariate methods considered below. In order to correct maps for the convergence of longitudinal lines at high latitudes we used Lambert equal area azimuthal projection.

## Statistical analysis

### *Species richness*

We calculated richness at two spatial scales, (1) throughout the entire region and (2) at the level of phytogeographical provinces (Cabrera & Willink, 1980). Richness was obtained by counting the total number of species (observed values), and through extrapolation (estimated values), by using parametric richness estimators (Mmean, Michaelis–Menten two-parameter hyperbola) and the nonparametric ICE (Colwell & Coddington, 1994; Colwell, 1997). With respect to the biogeographical analysis of concern, the most complete knowledge of the diversity of the group at all relevant spatial scales is required because of the bias that missing species may produce in the analyses of the assumed patterns (Blackburn &

Gaston, 1998). Therefore, it is important to confirm that the sampling effort has been sufficient, both overall and for each part of the geographical range. All calculations were completed using the EstimatesS 5.0 software (Colwell, 1997).

#### *Biogeography: climate, phytogeography and hosts × phorids*

**Cluster analysis.** Phorid species were grouped using cluster analysis (distance index of Jaccard combined with nearest neighbour grouping criterion; Legendre & Legendre, 1998) with respect to (1) climatic, (2) phytogeographic and (3) host data. The phytogeographical and host data were simplified for the analysis in the same way. In all cases distribution maps of phorid species were superimposed on phytogeographical and host maps. The entries in the 20 phorid species × 7 vegetation type matrix were either 0 or 1 depending on whether a given phorid did or did not occur within a specific phytogeographical region. Likewise, entries in the 20 phorid × 12 host ant matrix were either 0 or 1 depending on whether or not the phorid and potential host co-occur. In the case of the climatic analysis, a 0 or 1 was entered into each of the phorid species × climatic variable cells (20 × 15 in all) based on the following criteria: 0 was entered if the phorid occurs at locations which fall below the regional median experienced for that variable by all phorid species, and 1 if the phorid species occurs at locations recorded to be above the regional median experienced for that variable by all phorids. Finally, we did a cluster analysis combining the three types of variables. Thus in each case all entries were binary. Clusters were obtained with the PcOrd 4.0 software (MJM Software, 1999).

From each of the four cluster analyses developed as above, obvious clusters of phorids were identified and given arbitrary group numbers. Species which grouped together as cluster '1' or '2' with respect to the host ant analysis were accorded those same arbitrary numbers if they grouped together in subsequent analyses. Thus one phorid species might be designated 1,1,1,1 while another might be scored 1,4,1,2 to indicate their grouping with respect to each of the four analyses.

**Ordination.** To search for assemblages of phorids with respect to geographical distribution we carried out a correspondence analysis (CA) for the 20 phorid species across the 123 sample sites. To identify gradients in climate throughout the study region we performed principal components analysis (PCA) using the 123 sites × 15 climate variable matrix.

In order to test whether climatic variables might help explain the variation observed in the geographical patterns of phorid distribution, the above two matrices were analysed jointly with a canonical correspondence analysis (CCA). Ordination analyses were performed using PcOrd 4.0 (MJM Software, 1999).

Isocline maps of complex climatic variables from the CCA analysis were created by interpolating eigenvalues related to each of the first three axis. Each of the three resulting isocline maps was incorporated as a layer for direct geo-referencing to the map

of the 123 sites using GMT. Each site was given three numbers, each reflecting its position relative to the value of one of the main three CCA axis. Site scores with respect to an axis were reduced to + or – depending on whether the site fell above or below the zero isocline for that axis. Thus three ordered signs characterized each site. The resulting eight combinations reflect different phorid communities and were represented by shading values on the resulting map. Finally, 20 map layers representing the geographical records of each phorid species were compared sequentially to the CCA map just described to indicate the species composition of each community.

#### *Testing the Rapoport effect*

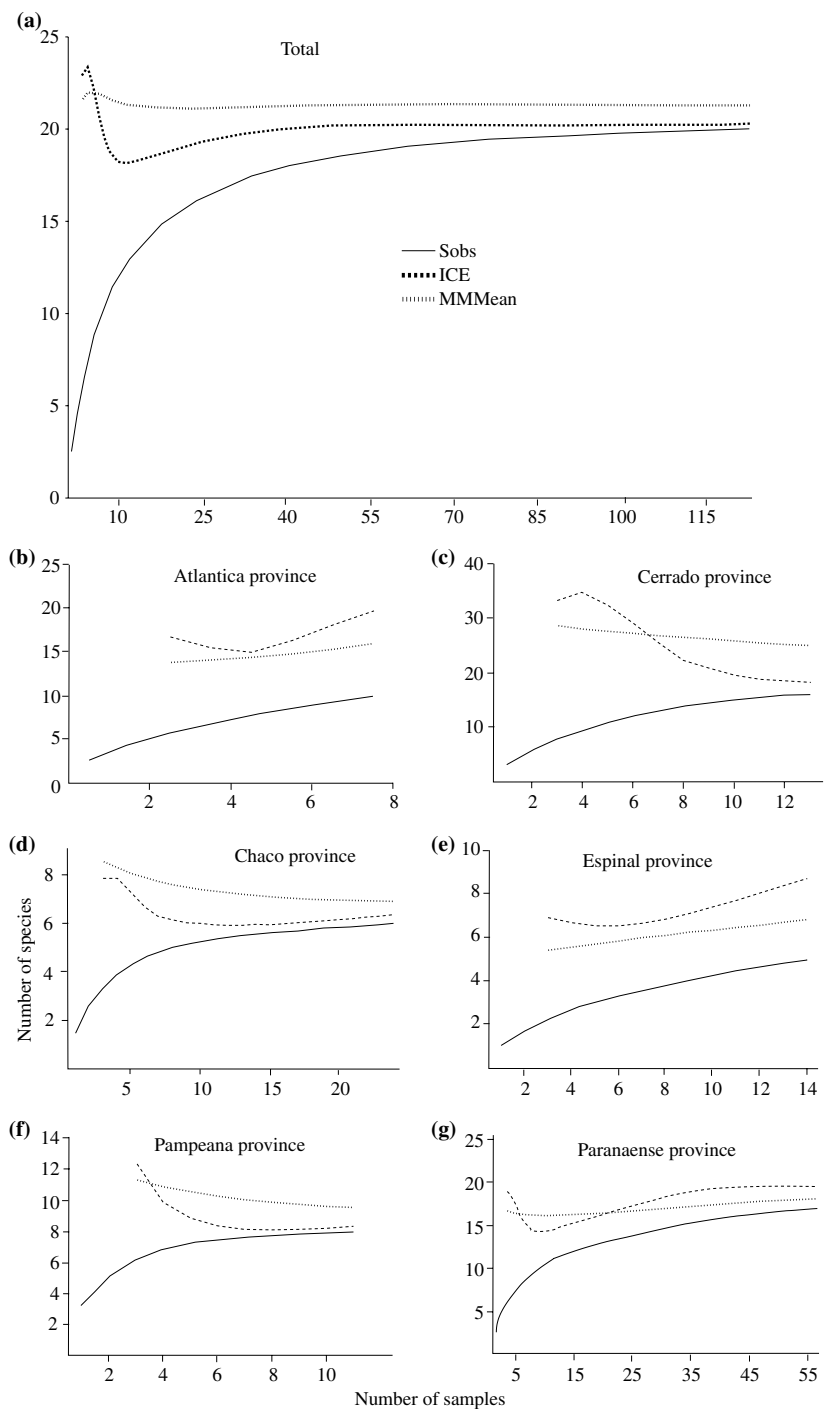
As indicated in the Introduction, the Rapoport rule predicts a positive correlation between mid-latitudinal points and the extent of latitudinal range or area occupied by species.

**Manipulation of data.** Each phorid species was considered as an independent point, located in space according to the mid-point of its north–south distribution (Rohde *et al.*, 1993). Although we analysed all data with longitude, as well as latitude, we found no significant effects of longitude (Bruzzone, 2004) and thus we focus here on latitudinal data only. In order to estimate the latitudinal range we measured the distance in kilometres between the north and south limits of distribution for each phorid species, corrected by spherical trigonometry (Kindred, 1998). Areas were calculated by using both 50 × 50 km and 250 × 250 km grid squares to evaluate whether the pattern emerged despite consideration of the area used. The area occupied by a species was the number of grids in which the species occurred at least one time. Borders of each grid were adjusted by considering the earth's curvature according to latitude (Kirvan, 1997; Kindred, 1998).

**Analysis.** Pearson correlation was used to test the Rapoport effect using observed data on the latitudinal mid-point against both latitudinal range and area. In addition, a null model of distribution for the 20 phorid species, against which the Rapoport rule could be tested, was generated from the one million randomizations using the raw distributional data (Colwell & Hurtt, 1994; Legendre & Legendre, 1998; Gotelli & Colwell, 2001).

We also calculated the nonparametric Spearman (Siegel, 1974) correlation between the three ways of determining range and area (latitudinal range, 50 km and 250 km grid) to explore if the different methods were ranking the data in a similar way.

Finally, we tested a possible mechanism that might account for the Rapoport rule by conducting a Mantel test (Legendre & Legendre, 1998) involving a multivariate comparison of two matrices of climatic variables. The first matrix represented the position of each species mid-point in a climatic gradient (equivalent to the latitudinal mid-point in the univariate Pearson correlation explained above) and the second matrix represented the breadth or amplitude of each species in the gradient (equivalent to the latitudinal range). The first matrix



**Figure 2** Species accumulation curves for the observed data set (Sobs) and for estimated values using the nonparametric (ICE) and the parametric (Michaelis–Menten, MMmed) richness estimators. Results are given for the overall area as well as by phytogeographical region. Curves were obtained after  $10^4$  randomizations.

was constructed by averaging extreme values of each of the 15 climatic variables within the distributional range of each species. Each data entry was then standardized with respect to the entire data set. Standardized data for each climatic variable were ranked from most to least favourable based on reasonable assumptions as to how phorids deal with those particular variables. The second matrix was constructed by subtracting the extreme values of each climatic variable for each phorid species. These values were then standardized as above. The significance of the Mantel test was assessed by running  $10^6$  randomizations.

## RESULTS

With respect to species richness, results depended on the level of analysis. Combining all 123 sites in the analysis, there were small differences between the total observed richness and the total estimated richness independent of the estimators used (Fig. 2). In the case of richness by region, estimates gave values above those actually observed (Fig. 2a–f), especially in those provinces least sampled. In better sampled regions (Chaco, Pampeana and Paranaense) rarefaction curves appeared to form an asymptote and to converge with observed values.

**Table 1** Parasitoid group classification according to results of cluster analyses by host, phytogeographical province, climate and all variables together. The final group represents the membership obtained by each parasitoid species given the criteria of sharing at least the same membership by three different criteria

<i>Pseudacteon</i>	Host	Phytogeographical province	Climate	All variables	Final group
<b>Cerrado</b>					
<i>affinis</i>	1	1	1	1	1
<i>dentiger</i>	1	1	1	1	1
<i>disneyi</i>	1	1	1	1	1
<i>fowleri</i>	1	3	1	1	1
<i>lenkoi</i>	1	3	1	1	1
<i>solenopsisidis</i>	1	1	2	1	1
<i>wasmanni</i>	1	1	1	3	1
<b>Widespread</b>					
<i>borgmeieri</i>	2	2	2	3	2
<i>cultellatus</i>	2	2	1	2	2
<i>curvatus</i>	2	2	2	2	2
<i>litoralis</i>	2	2	2	2	2
<i>nocens</i>	2	2	2	2	2
<i>nudicornis</i>	2	2	2	2	2
<i>obtusius</i>	2	2	2	2	2
<i>tricuspsis</i>	2	2	2	2	2
<b>Other</b>					
<i>bulbosus</i>	3	4	2	4	–
<i>conicornis</i>	1	1	4	3	–
<i>comatus</i>	2	1	2	3	–
<i>convexicauda</i>	2	1	1	2	–
<i>pradei</i>	1	1	4	3	–

With respect to grouping phorid species based on their association with host, phytogeographical province, climatic variables and all variables together (Table 1), a pattern emerged which can be related to other analyses below. The two major groups (1 & 2) defined by overlap with potential host species were largely supported by the other analyses. Group 1 was called the 'Cerrado Group' as its species are generally confined to tropical savanna vegetation. Group 2, was termed the 'Widespread Group', as its members occupy a great range of habitats and climates. The remaining species were difficult to categorize.

Correspondence analysis on phorid distributions by sample sites explained only 12.6%, 9.6% and 9.1% of the variance with the first, second and third axis respectively. In contrast, results from the PCA of climatic variables across the 123 sites explained 72.2% of the total variance. The first axis of the PCA (32%) represented a gradient of temperature and humidity (greater temperature and greater seasonal drought correlated with lower humidity). The second axis (27.1%) represented a gradient of low temperatures whereas the third axis (13.4%) represented a gradient of seasonality in drought.

The CCA analysis showed that the proportion of the explained variance in the phorid-by-site matrix was low (8.3%, 5.7%, 4.1% for the first, second and third axis respectively).

However, the ratio of the variance of the CA by the variance of CCA was high (for example, 65.8% for the first axis) and all three axes were significant after 1000 Monte Carlo randomizations. Thus despite the variation across sites and phorids, climatic variables significantly explained the observed assemblages of phorids.

The CCA analysis revealed two major gradients that explained most of the variance (Fig. 3). One gradient, shown by the arrow moving up from the lower left to upper right quadrants of Fig. 3a, moves from low minimum temperatures, high humidity and maritime type of climate towards high extreme temperatures, dry and continental climate. The second gradient is shown by the arrow moving from the lower right quadrat (low seasonality in precipitation) to the upper left (strong seasonality in precipitation). The biplot of axis 1 and axis 2 thus defines four groupings of phorid species.

1. In the upper right quadrat (Chaco-type climate) we find *tricuspsis* Borgmeier, *obtusius* Borgmeier, *curvatus* Borgmeier, *nocens* Borgmeier and *bulbosus* Brown.

2. In the upper left (savanna climate) we find *lenkoi* Borgmeier & Prado, *fowleri* Pesquero, *disneyi* Pesquero, *dentiger* Borgmeier, *affinis* Borgmeier, *cultellatus* Borgmeier, *nudicornis* Borgmeier, *solenopsisidis* Schmitz and *convexicauda* Borgmeier.

3. In the lower left (Maritime climate, seasonal precipitation) we find *borgmeieri* Schmitz, *comatus* Borgmeier, *wasmanni* Schmitz and *pradei* Borgmeier.

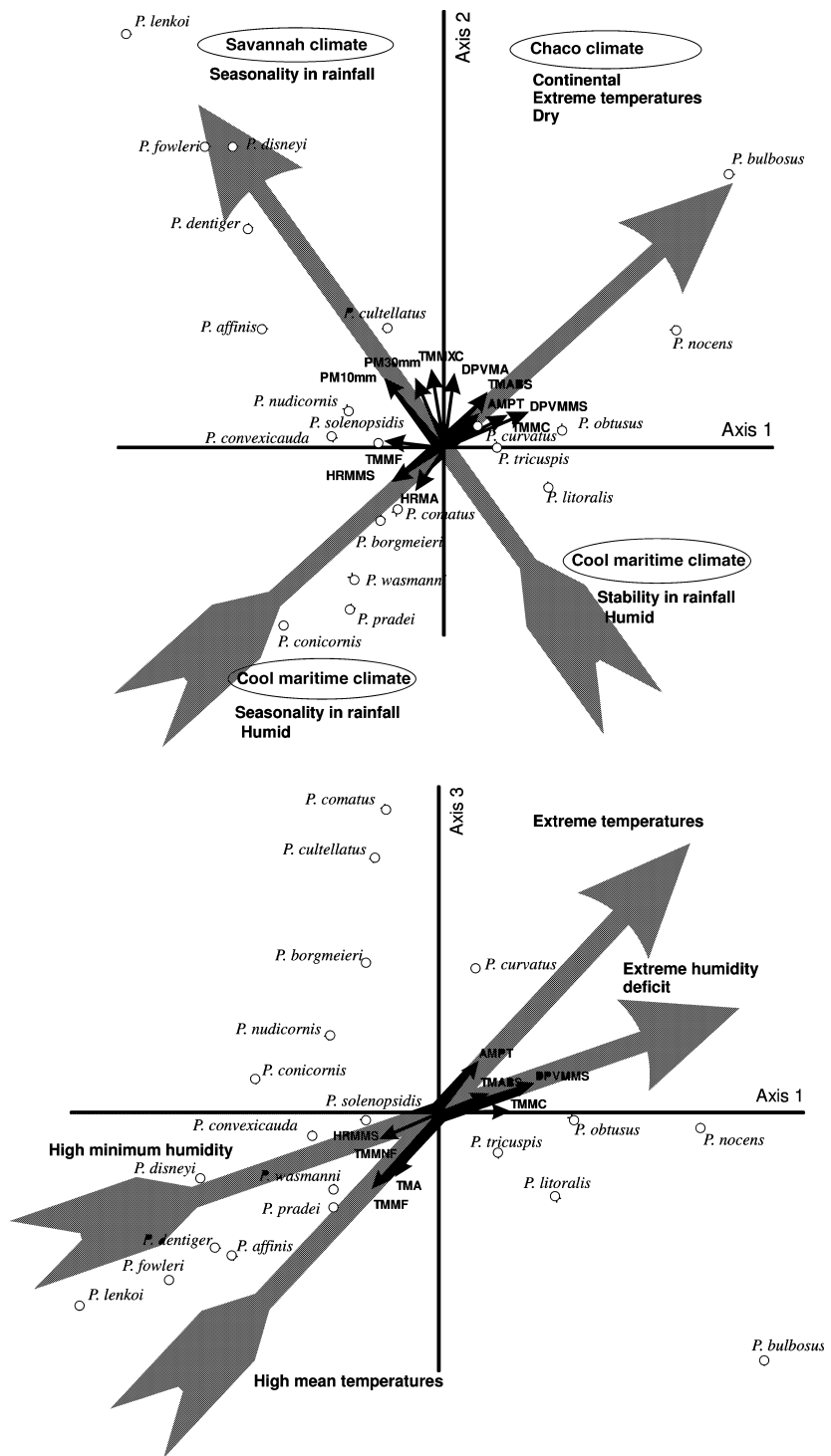
4. In the lower right (Cool Maritime, constant precipitation) we find only *P. litoralis* Borgmeier.

Turning to the CCA biplot of axis 1 and 3 (Fig. 3b), we describe two major gradients, both moving from lower left to upper right. The first represents the change from high temperatures and constancy to higher temperature extremes and variation. The second represents the transition from higher minimum humidity to lower values of minimum humidity. From this plot we define three major groupings of phorids. (1) Lower left quadrant (savanna climate) we found *P. lenkoi*, *fowleri*, *dentiger*, *affinis*, *pradei*, *wasmanni*, *disneyi*, *convexicauda* and *solenopsisidis*. (2) Upper right quadrat (Chaco-type climate) with *P. tricuspsis*, *litoralis*, *obtusius*, *nocens*, *curvatus* and *bulbosus* (the last one as an outlier). (3) Upper left quadrat (species with broadest distributions): those mentioned in (2) plus *P. comatus*, *cultellatus*, *borgmeieri*, *nudicornis* and *conicornis*.

### CCA map

Remarkably, the CCA map of eight phorid communities (Fig. 4) bears a striking resemblance to the phytogeographical provinces proposed by Cabrera & Willink (1980). Although we named the eight communities, which emerged from our analysis, in reference to existing names for vegetation zones of those areas, the phytogeographical maps played no role in generating our map. In contrast to large-scale phytogeographical maps for the region, our map of phorid assemblages indicates disjunctions in some communities (e.g. 'Pampa-Espinal' and 'Atlantica', Fig. 4).





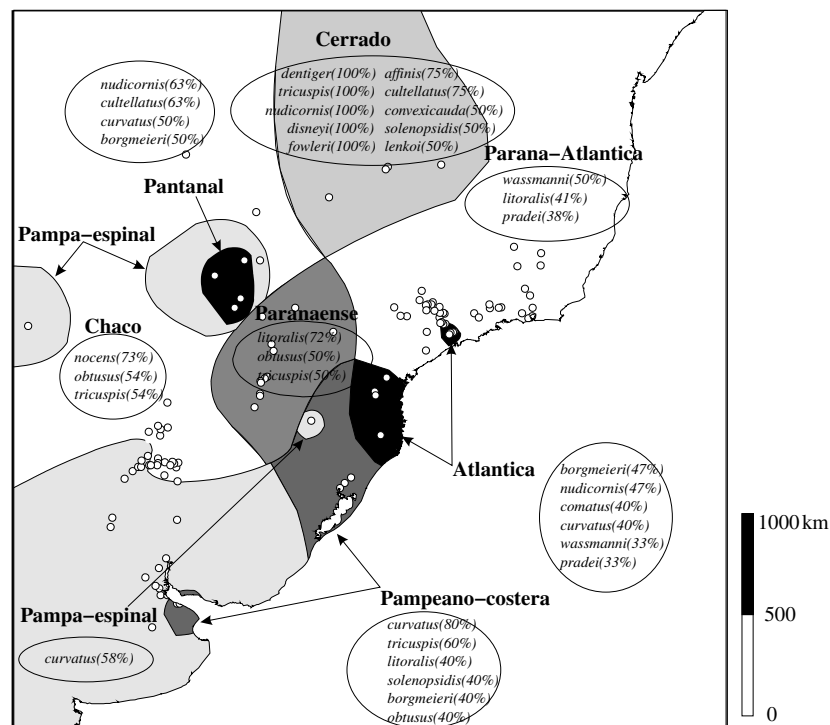
**Figure 3** First and second (top) and first and third (bottom) axes of the canonical correspondence analysis. Small black arrows indicate the relative importance of climatic variables whereas circles represent the ordination of parasitoid species. Big grey arrows represent the direction of climatic gradients determined by correlated climatic variables.

### Test of Rapoport's rule

The correlations between the mid-latitudinal point and area occupied (for both grid sizes) was positive and significant (50 km grid:  $r = 0.53$ ,  $P = 0.04$ ; 250 km grid:  $r = 0.56$ ,  $P = 0.04$ ) (Fig. 5). For the latitudinal range and mid-latitudinal point, the correlation was also positive but not significant ( $r = 0.55$ ,  $P < 0.08$ ). Although the areas estimated by the two grid methods gave different results, they were highly correlated

with each other ( $r = 0.95$ ,  $P > 0.01$ ) and with latitudinal range (50 km grid:  $r = 0.78$ ,  $P = 0.04$ ; 250 km grid:  $r = 0.86$ ,  $P < 0.01$ ). The estimated areas were either significantly smaller or did not differ from the areas expected if all species were randomly distributed (Table 2). The multivariate approach to testing the Rapoport rule using the Mantel test was also significant ( $r = 0.14$ ,  $P = 0.05$ ).

When data on estimated areas per phorid species are superimposed on CCA diagrams we find a clear relationship



**Figure 4** Map of parasitoid communities obtained by the combination of climatic variables according to the three first axis of the canonical correspondence analysis. Communities: Pampa-espinal (+,+,+), Chaco (+,+,-), Pampeano-Costera (+,-,+), Paranaense (+,-,-), Pantanal (-,+,+), Cerrado (-,+,+), Atlantica (-,-,+), Parana-Atlantica (-,-,-). Reported on the map are the percentage of sites (up to 33%) within a given 'community' which contained a given phorid species. The species represented in less than 33% of the sites are the following for each of the eight communities: Pampa-Espinal, *P. borgmeieri* (5%), *P. comatus* (5%), *P. cultellatus* (16%), *P. litoralis* (26%), *P. nocens* (16%), *P. nudicornis* (5%), *P. obtusus* (16%), *P. tricuspsis* (21%); Chaco, *P. bulbosus* (5%), *P. curvatus* (9%), *P. litoralis* (32%), *P. nudicornis* (5%); Pampeano-Costera, *P. comatus* (20%), *P. convexicauda* (20%), *P. cultellatus* (20%), *P. nocens* (20%), *P. nudicornis* (20%); Paranaense, *P. curvatus* (6%), *P. nocens* (11%), *P. pradei* (6%), *P. wasmanni* (11%); Pantanal, *P. comatus* (13%), *P. conicornis* (13%), *P. disneyi* (13%), *P. litoralis* (13%), *P. nocens* (13%), *P. obtusus* (13%), *P. pradei* (13%), *P. solenopsidis* (13%), *P. tricuspsis* (13%), *P. wasmanni* (25%); Cerrado, *P. borgmeieri* (25%), *P. wasmanni* (25%); Atlantica, *P. conicornis* (7%), *P. convexicauda* (13%), *P. cultellatus* (7%), *P. litoralis* (13%), *P. obtusus* (27%), *P. solenopsidis* (27%), *P. tricuspsis* (20%); Parana-Atlantica, *P. affinis* (9%), *P. borgmeieri* (16%), *P. comatus* (3%), *P. conicornis* (9%), *P. convexicauda* (3%), *P. curvatus* (19%), *P. dentiger* (6%), *P. disneyi* (3%), *P. fowleri* (3%), *P. nudicornis* (13%), *P. obtusus* (22%), *P. solenopsidis* (13%), *P. tricuspsis* (31%).

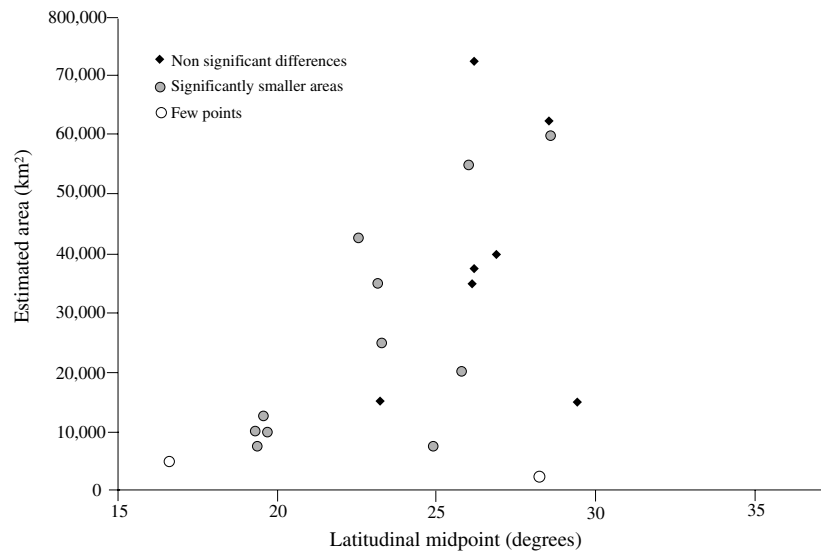
between the position of a species along the climatic gradient and the size of its area of distribution such that species with greater area are located in parts of the gradients with greater stress (Fig. 6).

## DISCUSSION

The total number of phorid species in the overall region studied summed to 20–21 species. For the overall region as well as for the phytogeographical provinces, the nonparametric ICE estimator tended to converge with the observed values more than the parametric Mmean. Overall, the estimated number of species did not differ substantially from the observed, but the same could not be said for separate phytogeographical sub-regions. Thus, only the Pampeana and Paranaense Provinces appeared to be sampled well enough to be confident of phorid species numbers. In the case of the Chaco Region only the wet part has been sampled adequately. Similarly for the Cerrado region, the southern portion has been better explored than the

north. These patterns can be explained by the fact that the 123 sites were not regularly distributed throughout the geographical range. Therefore, it is likely that increased sampling will lead to new additions to sub-region lists, including new phorid species and new host ant species.

Species categorized as 'type 1' (Table 1) (based on cluster analyses) were almost the same as those found in the upper and lower left corner of Fig. 3a,b and associate with savanna environment. Species categorized 'type 2' (Table 1) can be found in different quadrats of the ordination graphs, corresponding to varying environmental gradients. Therefore, the classification method failed to discriminate among species of broad geographical distribution ranges. This failure could be related to the fact that broadly distributed species share their distribution with that of their hosts, phytogeographical provinces and climate. Therefore, ordination methods were better than clustering techniques for discriminating among similarly distributed species. From these analyses, one group emerges as a robust and could be used for making decisions



**Figure 5** Symbols represent the mid-latitudinal points and areas estimated (using a  $50 \times 50$  km grid) for each parasitoid species. Diamonds indicate those parasitoid species for which their areas did not differ from random after randomizations (see Table 2) whereas grey circles represent parasitoid species that had significantly smaller ( $P < 0.05$ ) areas than predicted at random. Empty circles represent those few parasitoid species for which data were not sufficient to statistically test their distribution.

about introductions of these species for biological control. Species of the savanna group should be considered if the target climate for introduction of parasitoids has strong seasonality in rainfall, high mean temperatures and a high minimum humidity. Similarly, the Chaco group will be appropriate for continental climates, very dry and with extreme temperatures, although as this group involves widely distributed species, caution should be taken regarding the origin of the biotype (see below).

The ordination method allowed us to build maps and define phorid communities for the study area. The spatial distribution of these communities corresponded closely to the phytogeographical provinces defined by Cabrera & Willink (1980). This pattern is in fact not surprising. Vegetation responds to climate and, moreover, is determined by historical climatic patterns (Cabrera & Willink, 1980). This study showed that phorid communities are also determined by climate. Therefore, if both types of communities respond to

**Table 2** Areas, latitudinal ranges, mid-latitudinal points (ML) and number of collecting sites (#S) for each parasitoid species. Areas were estimated using two grid sizes,  $250 \times 250$  km and  $50 \times 50$  km. For each area and latitudinal range, the probability ( $P$ ) value is given for each parasitoid species

	Grid				Latitudinal extension			
	250 km ( $10^6$ km <sup>2</sup> )	$P$ (%)	50 km ( $10^6$ km <sup>2</sup> )	$P$ (%)	Range (degrees)	$P$ (%)	ML (degrees)	# S
<i>Pseudacteon</i>								
<i>affinis</i>	250.0	0.0639	12.50*	0.0166	5.90	0.0674	19.55	6
<i>borgmeieri</i>	562.5	0.1157	40.00	0.5439	18.02	0.7705	26.89	17
<i>bulbosus</i>	62.5	0.0000	2.50	0.0000	0.00	0.0000	28.21	1
<i>comatus</i>	250.0*	0.0234	15.00	0.0313	13.00	0.6857	29.4	7
<i>conicornis</i>	187.5*	0.0187	7.50*	0.0001	4.70	0.0562	24.85	5
<i>convexicauda</i>	312.5	0.3067	15.00	0.1974	13.18	0.7565	23.19	6
<i>cultellatus</i>	375.0	0.0786	20.00*	0.0178	18.32	0.9431	25.76	10
<i>curvatus</i>	875.0	0.2843	62.50	0.5289	14.77	0.1600	28.515	29
<i>dentiger</i>	125.0*	0.0006	10.00*	0.0073	6.40	0.1599	19.7	5
<i>disneyi</i>	187.5*	0.0188	10.00*	0.0071	5.67	0.1076	19.335	5
<i>fowleri</i>	125.0*	0.0028	7.50*	0.0024	5.67	0.1967	19.335	4
<i>lenkoi</i>	62.5*	0.0000	5.00*	0.0150	0.17	0.0436	16.585	2
<i>litoralis</i>	562.5*	0.0000	60.00*	0.0000	12.75*	0.0021	28.545	41
<i>nocens</i>	500.0	0.0298	35.00	0.0796	11.20	0.0786	26.1	17
<i>nudicornis</i>	625.0	0.2219	37.50	0.1125	19.40	0.9619	26.2	18
<i>obtusius</i>	687.5*	0.0051	55.00*	0.0060	19.83	0.9339	25.985	32
<i>pradei</i>	250.0*	0.0000	35.00*	0.0009	5.90*	0.0000	23.15	21
<i>solenopsidis</i>	437.5	0.0595	25.00*	0.0130	13.58	0.4456	23.29	13
<i>tricuspis</i>	875.0	0.0276	72.50	0.0374	19.40	0.8167	26.2	41
<i>wasmanni</i>	500.0*	0.0001	42.50*	0.0002	9.32*	0.0025	22.54	
Total	1526.5		202.50		19.83		25.985	123

\*Probability values were significantly different than random after 10,000,000 randomizations.

the same cause then they should be similarly distributed in space. This finding is important from an invasion ecology or biological control perspective because many predictions can be made about the composition and physiological amplitudes of different phorid communities depending on their affiliation to a particular phylogeographical region.

determining the distribution of insects or their food (Inouye, 2000). In lower elevation tropical climates, where frosts do not occur, seasonality of precipitation may play a similar role (Pinheiro *et al.*, 2002).

The Mantel test showed a significant multivariate relationship between the two aforementioned components of the Rapoport correlation. The use of the null model allowed us to identify significant patterns and to interpret them within the context of a stress gradient and thus to infer physiological tolerances of phorid species. Stating our results in classical terms: a positive relationship exists between the position of a species within the seasonality gradient (i.e. greater seasonality) and the size of its fundamental niche *sensu* Hutchinson (Pulliam, 2000). It is not surprising that species adapted to different portions of a multidimensional set of requirements will be found in a greater variety of environments and will end up with broader geographical distributions.

Our results suggest that those *Pseudacteon* species with broader geographical distributions have greater climatic tolerance. If these species are considered as biological control agents in exotic habitats, it would be wise to check first the environmental conditions present in the site of origin and compare it with potential release sites. For example, *P. tricuspis* from Sao Paulo State in Brazil has been successfully established on *S. invicta* in South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana and parts of Texas (Porter *et al.*, 1999; Gilbert & Patrock, 2002). These sites of introduction apparently do not offer serious environmental constraints to these species. On the contrary, this biotype of *P. tricuspis* has been established with much less success in the driest parts of *S. invicta* range in Texas (Gilbert & Patrock, 2002).

In short, *Pseudacteon* from the savanna and Chaco group can be introduced if the climate of the site of origin and release offer similar climatic stress. Otherwise, selecting phorid biotypes from species with broad ranges may allow better matching of climatic conditions as well as host biotypes (see Porter & Briano, 2000; Graham *et al.*, 2003). Future biogeographical analyses should monitor the success of introducing phorid fly biotypes from different climates.

## ACKNOWLEDGEMENTS

We thank the reviewers and Richard Patrock for their careful and thoughtful comments on this manuscript and the latter for providing insightful approaches for data analyses. Lloyd Morrison read the manuscript. G. Zaccardi, A. Sallenave, N. Gorosito and G. Zipeto helped gather data in the field in Argentina at different stages. Climatological data were gathered from the Argentinean Meteorological Service and NOAA. We are indebted to the Argentinean authorities (Reserva Ecológica Costanera Sur in Buenos Aires, INTA-Mercedes in Corrientes and Dirección Nacional de Flora y Fauna) and several private farms for giving us the necessary permits to collect specimens. Part of the field work and other work on the project was funded by the State of Texas fire ant initiative (FARMAAC) and Helen C. Kleberg and Robert J. Kleberg Foundation to LEG and by the Universidad Nacional de Quilmes to PJF. Analyses were performed thanks to funds obtained from the Universidad Nacional de Quilmes to PJF. PJF and OAB thank CONICET for their support.

## REFERENCES

- Ashton, K.G. (2001) Are ecological and evolutionary rules being dismissed prematurely? *Diversity and Distributions*, **7**, 289–295.
- Blackburn, T.M. & Gaston, K.J. (1998) Some methodological issues in macroecology. *American Naturalist*, **151**, 68–83.
- Blackburn, T.M. & Gaston, K.J. (2001) Linking patterns in macroecology. *Journal of Animal Ecology*, **70**, 338–352.
- Borgmeier, T. (1968) A catalogue of the Phoridae of the world (Diptera, Phoridae). *Studia Entomologica*, **11**, 1–367.
- Brown, J.H. (1995) *Macroecology*. The University of Chicago Press, Chicago, USA, 269 pp.
- Brown, B.V., Folgarait, P.J. & Gilbert, L.E. (2003) A new species of *Pseudacteon* Coquillett (Diptera: Phoridae) attacking *Solenopsis* fire ants (Hymenoptera: Formicidae) in Argentina. *Sociobiology*, **41**, 685–688.
- Bruzzzone, O.A. (2004) Análisis de patrones de distribución de los dípteros parasitoides del género *Pseudacteon*: una aproximación a través de tres escalas diferentes. PhD Thesis, Department of Biology, University of Buenos Aires, Argentina.
- Bunge, J. & Fitzpatrick, M. (1993) Estimating the number of species: a review. *Journal of the American Statistical Association*, **88**, 364–373.
- Cabrera, A.L. & Willink, A. (1980). *Biogeografía de América Latina*. Organización de los Estados Americanos, Washington DC, USA, 122 pp.
- Colwell, R.K. (1997) *EstimateS: statistical estimation of species richness and shared species from samples*. Version 5. <http://viceroy.eeb.uconn.edu/Estimates>
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society (Series B)*, **345**, 101–118.
- Colwell, R.K. & Hurtt, G.C. (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist*, **144**, 570–595.
- Danks, H.V. (1996) The wider integration of studies on insect cold-hardiness. *European Journal of Entomology*, **93**, 369–382.
- Disney, R.H.L. (1994) *Scuttle flies: the Phoridae*. Chapman & Hall, London.
- Farji Brener, A.G. & Ruggiero, A. (1994) Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical range sizes. *Journal of Biogeography*, **21**, 391–399.
- Feener, D.H.J. & Brown, B.V. (1992) Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae), in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae). *Annals of the Entomological Society of America*, **80**, 148–151.
- Fisher, B.L. (1999) Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar. *Ecological Applications*, **9**, 714–731.
- Folgarait, P.J. & Gilbert, L.E. (1999) Phorid parasitoids affect foraging under different availability of food in Argentina. *Ecological Entomology*, **24**, 1–11.
- Folgarait, P.J., Bruzzzone, O.A., Patrock, R.J.W. & Gilbert, L.E. (2002) Developmental rates and host specificity for *Pseudacteon* parasitoids (Diptera: Phoridae) of fire ants (Hymenoptera: Formicidae) in Argentina. *Journal of Economic Entomology*, **95**, 1151–1158.
- Folgarait, P.J., Bruzzzone, O.A. & Gilbert, L.E. (2003) Seasonal patterns of activity among species of black fire ant parasitoid flies (*Pseudacteon*: Phoridae) in Argentina explained by analysis of climatic variables. *Biological Control*, **28**, 368–378.
- Fowler, H.G., Pesquero, M.A., Campiolo, S. & Porter, S.D. (1995) Seasonal activity of species of fire ants in Brazil. *Científica*, **23**, 367–371.
- Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998) Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution*, **13**, 70–74.
- Gauld, I.D. (1986) Latitudinal gradients in ichneumonids species-richness in Australia. *Ecological Entomology*, **11**, 155–161.
- Gilbert, L.E. & Morrison, L.W. (1997) Patterns of host specificity in *Pseudacteon* parasitoid flies (Diptera, Phoridae) that attack *Solenopsis* fire ants (Hymenoptera, Formicidae). *Environmental Entomology*, **26**, 1149–1154.
- Gilbert, L.E. & Patrock, R.J.W. (2002) Phorid flies for the biological suppression of imported fire ants in Texas: region specific challenges, recent advances and future prospects. *Southwestern Entomologist*, **25**, 7–17.
- Golden Software (2001) *Surver version 8*. Golden Software, Inc., Golden, CO, USA.
- Gotelli, J.N. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Graham, L.C., Porter, S.D., Pereira, R.M., Dorough, H.D. & Kelley, A.T. (2003) Field releases of the decapitating fly *Pseudacteon curvatus* (Diptera: Phoridae) for control of

- imported fire ants (Hymenoptera: Formicidae) in Alabama, Florida, and Tennessee. *Florida Entomologist*, **86**, 334–339.
- Hawkins, B.A. (1990) Global patterns of parasitoid assemblage size. *Journal of Animal Ecology*, **59**, 57–72.
- Hodkinson, I.D., Bird, J., Miles, J.E., Bale, J.S. & Lennon, J.J. (1999) Climatic signals in the life history of insects: the distribution and abundance of heather psyllids (*Strophingia* spp.) in the UK. *Functional Ecology*, **13**, 83–95.
- Inouye, D.W. (2000) The ecological and evolutionary significance of frosts in the context of climate change. *Ecology Letters*, **3**, 457–463.
- Isaaks, E.H. & Srivastava, R.M. (1989) *Applied geostatistics*. Oxford University Press, Oxford.
- Kindred, D. (1998) *Dist - find great-circle distance between two points on earth's surface* <http://www.indo.com/cgi-bin/dist>.
- Kirvan, A.P. (1997) *Latitude/Longitude, NCGIA Core Curriculum in GIScience*. <http://www.ncgia.ucsb.edu/gisc/units/u014/u014.html>
- Koleff, P. & Gaston, K.J. (2001) Latitudinal gradients in diversity: real patterns and random models. *Ecography*, **24**, 341–351.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd edn, Elsevier, Amsterdam.
- Lobo, J.M. & Martín-Piera, F. (2002) Searching for a predictive model for species richness of Iberian dung beetle based on spatial and environmental variables. *Conservation Biology*, **16**, 158–173.
- Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology*, **83**, 689–702.
- Lyons, S.K. & Willig, M.R. (1997) Latitudinal patterns in range size: methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos*, **79**, 568–580.
- May, R.M. (1988) How many species on earth? *Science*, **241**, 1441–1449.
- MJM Software, (1999) *PCOrd version 4*. MJM Software, Oregon, USA, 237 pp.
- Morrison, L.W., Dall'Aglio-Holvorcem, C.G. & Gilbert, L.E. (1997) Oviposition behavior and development of *Pseudacteon* flies (Diptera: Phoridae) parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). *Environmental Entomology*, **26**, 716–724.
- NOAA (1991) *Climates of the world*. NOAA, Asheville, NC, USA.
- Orr, M.R., Seike, S.H., Benson, W.W. & Gilbert, L.E. (1995) Flies suppress fire ants. *Nature*, **373**, 292–293.
- Orr, M.R., Seike, S.H. & Gilbert, L.E. (1997) Foraging ecology and patterns of diversification in dipteran parasitoids of fire ants in south Brazil. *Ecological Entomology*, **22**, 305–314.
- Pesquero, M.A., Campiolo, S., Fowler, H.G. & Porter, S.D. (1996) Diurnal patterns of ovipositional activity in two *Pseudacteon* fly parasitoids (Diptera: Phoridae) of *Solenopsis* fire ants (Hymenoptera: Formicidae). *Florida Entomologist*, **79**, 455–457.
- Pinheiro, F., Diniz, I.R., Coelho, D. & Bandeira, M.P.S. (2002) Seasonal pattern of insect abundance in the Brazilian Cerrado. *Austral Ecology*, **27**, 132–136.
- Porter, S.D. (1998) Biology and behavior of *Pseudacteon* decapitating flies (Diptera: Phoridae) that parasitize *Solenopsis* fire ants (Hymenoptera: Formicidae). *Florida Entomologist*, **81**, 1–18.
- Porter, S.D. (2000) Host specificity and risk assessment of releasing the decapitating fly *Pseudacteon curvatus* as a classical biocontrol agent for imported fire ants. *Biological Control*, **19**, 35–47.
- Porter, S.D. & Briano, J. (2000) Parasitoid-host matching between the little decapitating fly *Pseudacteon curvatus* from Las Flores, Argentina and the black fire ant *Solenopsis richteri*. *Florida Entomologist*, **83**, 422–427.
- Porter, S.D. & Pesquero, M.A. (2001) Illustrated key to *Pseudacteon* decapitating flies (Diptera: Phoridae) that attack *Solenopsis saevissima* complex fire ants in South America. *Florida Entomologist*, **84**, 691–699.
- Porter, S.D., Nogueira de Sá, L.A., Flanders, K & Thompson, L. 1999. Field releases of the decapitating fly, *Pseudacteon tricuspidis*. *Imported Fire Ant Conference*, Charleston, South Carolina, p. 102.
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- Quicke, D.L.J. & Kruft, R.A. (1995) Latitudinal gradients in North American braconid wasp species richness and biology. *Journal of Hymenoptera Research*, **4**, 194–203.
- Rohde, K. (1999) Latitudinal gradients in species diversity, and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? *Ecography*, **22**, 593–613.
- Rohde, K., Heap, M. & Heap, D. (1993) Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *The American Naturalist*, **142**, 1–16.
- Rudloff, W. (1981) *World climates*. Wissenschaftliche Verlagsgesellschaft mbh, Stuttgart.
- Ruggiero, A. (1999) Búsqueda de patrones en macroecología: la regla de Rapoport. *Ecología Austral*, **9**, 45–63.
- Sanders, N.J. (2002) Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography*, **25**, 25–32.
- Servicio Meteorológico Nacional (1992) *Estadísticas Climatológicas 1981–1990*. 1st edn. Fuerza Aérea Argentina, Buenos Aires.
- Siegel, S. (1974) *Estadística no paramétrica*. Trillas, México, DF, Mexico.
- Sime, K.R. & Brower, A.V.Z. (1998) Explaining the latitudinal gradient anomaly in ichneumonid species richness: evidence from butterflies. *Journal of Animal Ecology*, **67**, 387–399.
- Stadler, B. (2002) Determinants of the size of aphid-parasitoid assemblages. *Journal of Applied Entomology*, **126**, 258–264.
- Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist*, **133**, 240–256.
- Trager, J.C. (1991) A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae). *Journal of New York Entomological Society*, **99**, 141–198.

Wessel, P. & Smith, W.H.F. (1995) *The generic mapping tools (GMT) version 3.0. Technical reference and cookbook*. SOEST/NOAA, <ftp://pahoehoe.soest.HAWAII.edu/pub/gmt>

Willott, S.J. (2001) Species accumulation curves and the measure of sampling effort. *Journal of Applied Ecology*, **38**, 484–486.

## BIOSKETCHES

**Patricia J. Folgarait** is Associate Professor of Biology, University of Quilmes, Argentina, and co-director of a Research Program on Biological Interactions. She is a community ecologist interested in all types of interactions involving ants, especially those relating to pest ants and their biological control.

**Octavio Bruzzone** and **Marcos Pesquero** are recently graduated PhD students, interested in spatial ecology and parasitoid taxonomy, respectively.

**Sanford Porter**, a Research Entomologist for the USDA's Agricultural Research Service, studies the ecology and behaviour of ants. He currently focuses his efforts on fire ant biocontrol.

**Lawrence E. Gilbert** is Professor of Integrative Biology and Director of Brackenridge Field Laboratory, University of Texas-Austin. He is interested in behavioural and evolutionary aspects of species interactions in insect communities from butterflies and host plants to phorid flies and host ants.

---

Editor: Philip Stott